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New Data on Tropical Eastern Pacific Chromodorididae (Nudibranchia: Doridina) with Description of a New Species of *Mexichromis* Bertsch, 1977

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Specimens of a small red-spotted species of chromodorid have been collected from southern México, Costa Rica, Panamá, Malpelo Island, Colombia and the Galápagos Islands. Comparison with described species reveals that they are juveniles of *Chromodoris banuanni* Bertsch, 1970. Specimens studied here exhibit considerable variation both ontogenetically and geographically. Mature specimens share characteristics with species attributed to the genus *Glossodoris*, and the systematic status of this species is reviewed and revised. Another species of chromodorid nudibranch is described from the tropical eastern Pacific. *Mexichronuis tica* sp. nov. has been collected from Costa Rica and the Galápagos Islands. It differs from other eastern Pacific, Atlantic, and Indo-Pacific species in the genus in several important regards: (1) it has a white body color with a medial opaque white line and successive submarginal opaque white and orange marginal bands; (2) it has few large mantle glands distributed along the entire mantle margin; and (3) it has a vestigial rachidian row of teeth and variously denticulate inner, middle and outer lateral radular teeth.

Resumen

Ejemplares de una especie de cromodórido de pequeño tamaño con puntos rojos han sido recolectados en el sur de México, Costa Rica, Panamá, Isla Malpelo, Colombia e Islas Galápagos. Comparaciones detalladas con otras especies descritas muestran que son especimenes juveniles de *Chromodoris baumanni* Bertsch, 1970. Los ejemplares estudiados presentan una considerable variabilidad ontogenética y geográfica. Los ejemplares maduros comparten características atribuidas al género *Glossodoris* y el estatus taxonómico de ésta especie es revisado y discutido. Otra especie de nudibranquio cromodórido se describe del Pacífico Este tropical. *Mexichronuis tica* sp. nov. ha sido recolectada en Costa Rica y las Islas Galápagos. Se diferencia de otras especies del género del Pacífico Este, Atlántico e Indopacífico por varios aspectos importantes: (1) Esta especie tiene un cuerpo blanco con una línea blanca opaca media y sucesivas bandas submarginales blanco opaco y naranja; (2) glándulas del manto de gran tamaño distribuidas por todo el borde del manto; (3) y una fila de dientes radulares raquídeos vestigiales así como varios dientes medios y marginales denticulados.

The chromodorid nudibranchs of the eastern Pacific Ocean have been reviewed by Bertsch (1977, 1978a-c). Since then only four additional species of chromodorid have been described from the eastern Pacific (Gosliner and Bertsch 1988; Ortea, Bacallado and Valdés 1992). Gosliner and Bertsch (1988) described Mexicliromis amalguae from the Pacific coast of Baja California. Ortea et al. (1992) described three new species, Berlanguella scopae, Chromodoris ruzafai and Thorunna talaverai from the Galápagos. They also identified specimens of another chromodorid from the Galápagos Archipelago as supposedly Noumea haliclona (Burn, 1957). This species bears a striking resemblance to specimens of Chromodoris banmanni Bertsch, 1970, and its status is discussed here. Our recent field collections from Costa Rica, Baja California, the Galápagos Islands, and Panamá have provided additional material of this species. Detailed anatomical examination of variation in this species is warranted in order to evaluate its systematic status. A second species, collected from Costa Rica and the Galápagos, appears to be undescribed. Its external morphology differs markedly from other described eastern Pacific chromodorids. This paper describes and reviews the systematic placement of these two species.

SPECIES DESCRIPTIONS

Mexichromis tica Gosliner, Ortea, and Valdés, sp. nov.

(Figs. 1A, 2-3)

TYPE MATERIAL.— HOLOTYPE: CASIZ 170938, NE side Isla Darwin, Islas Galápagos, Ecuador, 23 m depth, 13 May 1994, leg. T.M. Gosliner. PARATYPES: CASIZ 097511, one specimen, dissected, NE side Isla Darwin, Islas Galápagos, Ecuador, 23 m depth, 13 May 1994, leg. T.M. Gosliner. INBIO CRI 001486639, two specimens, dissected, Bajo del Diablo, Isla del Caño, Costa Rica. 18 April 1996, leg. E. Mollo.

ETYMOLOGY.— Mexichromis tica is named for the vernacular name "tico," which signifies a native of Costa Rica.

DISTRIBUTION.— This species is known from Costa Rica and the Galápagos Islands (present study).

EXTERNAL MORPHOLOGY .- The living animals (Fig. 1A) are translucent white. The pink viscera, showing through the translucent white dorsum, give the animal an overall pinkish appearance. A broad, opaque, white longitudinal band extends mid-dorsally from between the rhinophores to the anterior edge of the branchial cavity. The mantle margin is translucent white. A broad, opaque, white band is present submarginally along the mantle edge. Inside the white band, there is a band of orange or yellow that may be either continuous or interrupted. The posterior end of the foot is translucent white with a medial white stripe. An orange spot is present near the middle of the white stripe. The rhinophores have a translucent white base and an orange apex. The gill pinnae are uniformly translucent white.

Living animals are 3-6 mm in length. The dorsal surface of the mantle is covered with minute conical tubercles. The mantle is elongately oval and straight along its entire edge. The margin that overhangs the body is wide, nearly half of the total mantle width. The posterior end of the foot is triangular and extends some distance behind the posterior end of the mantle. Around the mantle margin are several rows of large, irregularly-shaped mantle glands (Fig. 3A). The glands of the largest specimen are more numerous with smaller glands situated between the larger ones. Triangular spicules are visible between the mantle glands around the margins of the mantle. The rhinophore stalk is short and the bulb bears 7-10 lamellae in the specimens examined. There are 4 unipinnate to bipinnate branchial leaves in the material examined. The foot is relatively narrow. The head and mouth are well-developed with a triangular oral tentacle on either side of the mouth.

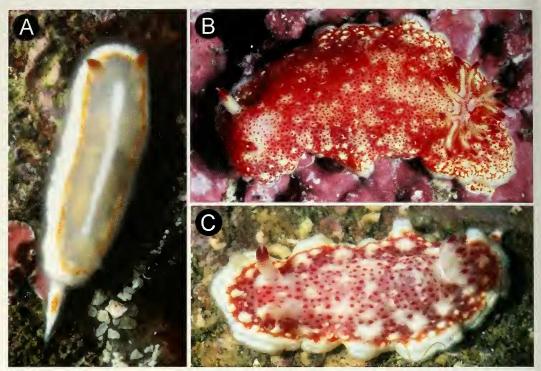


FIGURE 1. Living animals. A. *Mexichromis tica* sp. nov, holotype (CASIZ 097511), from Isla Wolf, Galápagos Islands, photo by T.M. Gosliner. B. *Glossodoris baumanni* (Bertsch, 1970), adult specimen, 33 mm length, from San Pedrillo, Costa Rica, photo by T.M. Gosliner. C. *Glossodoris baumanni* (Bertsch, 1970), juvenile specimen, 12 mm length, from San Pedrillo, Costa Rica, photo by T.M. Gosliner.

BUCCAL ARMATURE.— At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 2D) are short and broad with a broad apex bearing 3–7 irregular shaped denticles. The radular formula is difficult to determine owing to the broadly overlapping teeth. A vestigial rachidian row of teeth is present in one specimen (CASIZ 097511, Fig. 2A), but it appears to be absent in the other two individuals examined (INBIO CRI 001486639). The rachidian row of teeth in the one specimen consists of teeth with only a short narrow cusp. The innermost lateral teeth (Fig. 2A) have a broad base with a series of 4–6 curved, triangular denticles along the inner margin. There is no primary cusp and most of the denticles are equal in size with the exception of the outermost, which is smaller than the others. The lateral teeth from the middle of the radular row are short and curved (Fig. 2C) and bear 4–6 curved, triangular denticles on the outer side of the teeth. The more basal denticles are smaller than the others, but there is no primary cusp on any of these teeth (acuspidate, *sensu* Bertsch, 1977). The 4–5 outermost lateral teeth (Fig. 2B) are broad and spatulate and are thinly chitinized. They bear 16–20 thin, elongate denticles along the margin.

REPRODUCTIVE SYSTEM.— (Fig. 3B) The ampulla is short, thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens curves over the bursa copulatrix and narrows into a short ejaculatory segment. This muscular portion narrows and again widens into the short penial bulb. The penial bulb shares a common atrium with the vagina. The distal end of the vas deferens is devoid of penial hooks. The female gland mass consists of the

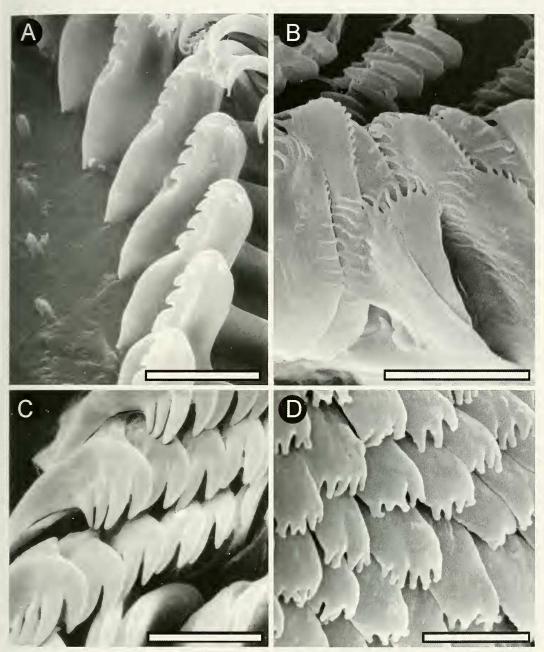


FIGURE 2. *Mexichromis tica* sp. nov., scanning electron micrographs. A. Rachis and inner lateral teeth (paratype, CASIZ 097511), scale bar = 10 μ m. B. Outer lateral teeth, (paratype, CASIZ 097511), scale bar = 10 μ m. C. Lateral teeth from the central portion of half-row, (paratype, CASIZ 097511), scale bar = 7.5 μ m. D. Jaw rodlets, (paratype, INBIO CRI 001486639), scale bar = 5 μ m.

large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively thin and straight. It is widest nearest its junction with the penis. The elongate, club-shaped receptaculum seminis has a recurved duct that joins directly to the base of the thin-walled, spherical bursa copulatrix. The vagina emerges near the base of the bursa. The thin uterine duct emerges from the middle of the thin vagina. The uterine duct is short and curved and enters the female gland mass near the albumen gland.

DISCUSSION.— Rudman (1984) reviewed the genera of chromodorid nudibranchs and concluded that *Mexichromis* Bertsch, 1977, represents a valid genus. *Mexichromis* is characterized by having a few large mantle glands, acuspidate (Bertsch 1977) or multicuspidate (Rudman 1984) radular teeth, and a ramified vestibular gland (Rud-

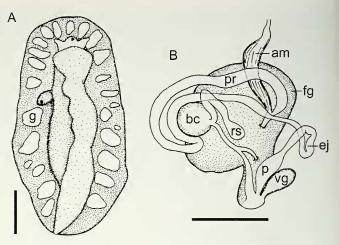


FIGURE 3. *Mexichromis tica* sp. nov., A. Ventral view of holotype (CASIZ 097511) showing distribution of mantle glands, g = mantle gland, scale bar = 2 mm. B. Reproductive system, am = ampulla; bc = bursa copulatrix; ej = ejaculatory duct; fg = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; vg = vestibular gland, scale bar = 1 mm.

man 1984). In the eastern Pacific, *Mexichromis* is represented by *M. antonii* (Bertsch, 1976), *M. porterae* (Cockerell, 1901), *M. tura* (Marcus and Marcus, 1967) and *M. amalguae* Gosliner and Bertsch, 1988.

Mexichromis francoisae (Bouchet, in Bouchet and Ortea, 1980) is known from the eastern Atlantic of Senegal (Bouchet and Ortea 1980) and the Cape Verde Islands (Ortea 1988). This species was transferred to the genus *Mexichromis* by Ortea et al. (1996). Ortea et al. (1996)also described *M. molloi* Ortea and Valdés. 1996, from Venezuela. These eastern Pacific and Atlantic species all have a blue ground color with yellow or white longitudinal lines or marginal bands. Rudman (1984) suggested that *Chromodoris kempfi* Marcus, 1970, may be a species of *Mexichromis*, but little is known of its anatomy. Its greenish body color with a yellow marginal band with black markings differs markedly from the color of *M. tica*.

Several Indo-Pacific species, *M. festiva* (Angas, 1864), *M. mariei* (Crosse, 1872), *M. macropus* Rudman, 1983, and *M. multituberculata* (Baba, 1953), have an opaque white body color with large purple tubercles on the notum. Additional purple, yellow or orange pigment may also be present.

The color pattern of *M. tica*, with a transluscent white ground color with opaque white and yellow submarginal bands. is unique for this species. Of the species of *Mexichromis* that have been studied, only *M. amalgnae* and *M. tica* are known to possess a vestigial rachidian tooth. However, a rachdian row of teeth may be present or absent in *M. tica. Mexichromis tica* is unique among members of *Mexichromis* in having multidenticulate to pectinate outer lateral teeth. In the remaining taxa, the outer lateral teeth are similar in shape to the midlateral teeth.

The reproductive system has been described in detail for *Mexchromis macropus*. *M. porterae*, *M. tura*, *M. francoisae*, *M. molloi*, and *M. amalguae* (Rudman 1984; Gosliner and Bertsch 1988; Ortea et al. 1996). In these six species, the vestibular gland consists of multiple lobes, whereas in *M. tica* it is simply ovoid.

Inclusion of *M. tica* in *Mexichromis* requires modifying the boundaries of the taxon to include species with pectinate outer lateral teeth and a simple vestibular gland. *Mexichromis tica* is tenta-

tively placed in *Mexichromis* until a more comprehensive phylogenetic study of the Chromodoridiae is undertaken.

Glossodoris baumanni (Bertsch, 1970)

(Figs. 1B-C. 4-5)

Chromodoris norrisi Farmer, 1963: Marcus and Marcus, 1967:170-173, fig. 24, misidentification.

Chromodoris baumanni Bertsch, 1970:8, figs. 3–13; Sphon and Mulliner, 1972:150; Bertsch, 1978a:307, fig. 3a, 4. 10–12; Bertsch, in Kerstitch, 1991:57; Debelius, 1996:212, lower figure.

Nounea haliclona (Burn, 1957): Ortea. Bacallado and Valdés, 1992:62–65, figs. 19–20, pl. 1E, misidentification.

Glossodoris baumanni, (Bertsch, 1970), comb. nov.

MATERIAL EXAMINED.- CASIZ 074004, one specimen, dissected, s side of Pulmo Point, Cabo Pulmo, Baja California Sur, México, 13 m. depth, 22 January 1984, leg. H. Bertsch and L. Aguilar. INBIO CRI 001486926. one specimen, Bahía Hachal, Costa Rica, 8 December 1995. INBIO CRI 001486927. two specimens, Punta Uvita, Costa Rica, 14 April 1996. CASIZ 075179, one specimen, Isla del Coco, Costa Rica, 13 m. depth, 24 March 1989, leg. K. Kaiser WAM 102-95. one specimen, Isla de Cocos, Costa Rica, 28 March 1997, leg. C. Bryce. WAM 106-95, one specimen, Isla de Cocos, Costa Rica, 23 March 1997, leg. K. Kaiser. CASIZ 088147, five specimens, one dissected, sea stack, off Isla Ladrones, Gulf of Chriquí, Panamá, 14 m. depth, 14 April 1993, leg. T.M. Gosliner. CASIZ 088150, three specimens, Punta David, se side of Isla Jicarón, Gulf of Chiriquí, Panamá. 13 m. depth. 17 April 1993, T.M. Gosliner. CASIZ 088203, four specimens, point W of anchorage, Islas Secas, Gulf of Chiriquí, Panamá, 13 m. depth, 22 April 1993, leg. T.M. Gosliner. CASIZ 088227, one specimen, off Rocas Tiburón, off Isla Brincano, Gulf of Chiriquí, Panamá, 23 April 1993, leg. T.M. Gosliner. CASIZ 088161, two specimens, se side of Isla Jicarón, Gulf of Chiriquí, Panamá, 16 April 1993, leg. T.M. Gosliner. CASIZ 097512, one specimen, NE side Isla Darwin, Islas Galápagos, Ecuador, 22 m. depth, 13 May 1994, leg. T.M. Gosliner. CASIZ 071429, one specimen, Isla Santiago, Islas Galápagos, Ecuador, intertidal zone, 19 February 1988, leg. K. Kaiser. WAM S1164, one specimen, Isla Malpelo, Colombia, 13 m depth, 26 March 1998, leg. C. Bryce. One specimen, Puerto Egas, Isla Santiago, Islas Galápagos, 18 March 1991, leg. J. Ortea. One specimen, Isla Genovesa, Islas Galápagos, 8 March 1991, leg. J. Ortea.

DISTRIBUTION.— This species is known from the Gulf of California, Baja California Sur (Bertsch, 1970, 1978a; present study) México; Sayulita, Nayarit, México; several localities in Costa Rica. Panamá, the Galápagos Islands and from Isla Malpelo, Colombia (present study).

NATURAL HISTORY.— *Glossodoris baumanni* is found in relatively shallow water on rocky reefs. In Costa Rica and Panamá, it is one of the most commonly occurring opisthobranchs from the intertidal zone to 20 meters depth.

EXTERNAL MORPHOLOGY.— The living animals (Fig. 1B–C) are brightly colored with a network of purple to red and opaque white pigment. There is a broad yellowish white or light gray band around the mantle, just inside the translucent white margin. The inside edge of the white border is very irregular and slightly convoluted with opaque white, with 1–5 rows of rounded mantle glands extending into the brick red central part of the body (Fig. 1C). There are numerous purplish red spots, each surrounded by a broad purple-gray or yellowish ring all over the central brick red patchwork. Specimens from Baja California generally lack red pigment between the red spots and the notum is opaque white. More mature specimens south of Baja California have dense red pigment between the red spots (Fig. 1B). An identical pattern is present on the surface of the foot. The majority of these spots are joined together forming patches of varying sizes. The rhinophores have an opaque white base and a broad purple band just below the opaque white apex. The gill pinnae are also opaque white with purple apices. Scattered red pigment spots are present on the innner and outer surfaces of the gill rachis.

The living animals are 9–65 mm in length. The mantle is elongately ovoid and folds down over the sides of the body forming a series of permanent undulations of the mantle edge. These undulations are more pronounced in more mature specimens. The margin that overhangs the body is wide, nearly half of the total mantle width. The posterior end of the foot is triangular and extends some distance behind the posterior end of the mantle. Immediately interior to the mantle margin are 1–5 rows of irregularly distributed, rounded mantle glands (Fig. 5A). The mantle glands are more dense and smaller near the margin. The interior glands are larger and have an irregular lobed shape. The rhinophore stalk has 9–22 lamellae in the specimens examined. There are 6–15 unipinnate branchial leaves in the material examined. In some of the larger speciments a few of the posterior gills are not entirely separate to the base, but have been counted as distinct gill branches. In the larger specimens the branchial leaves form a spiral on either side and the gill has been observed to vibrate slowly.

BUCCAL ARMATURE.— The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 4D) are elongate, curved and have a bifid apex. The radular formula is $61 \times 39.1.39$. in one 20 mm specimen examined (CASIZ 088203) and a 12 mm specimen $33 \times 21.0.20$. A rachidian row of teeth is present in one specimen, but absent in the other four individuals examined. Examination of the holotype and paratype radula revealed similar variation in the presence and absence of a rachidian row of teeth, with the holotype lacking a rachdian row, while the paratype has a row of rachidian teeth. The innermost lateral teeth (Fig. 4A) are arched with a short cusp. There are 1-2 triangular denticles on the inner side of the tooth. The outer side has 1-3 denticles. In the radulae with the rachidian tooth present, it is apparent that the rachidian tooth actually represents a portion of the inner lateral tooth where the inner denticle was present. The second through fourth laterals have 3-4 denticles on the outer side of each tooth. The lateral teeth from the middle of the radular row are far more elongate (Fig. 4B) and bear 4-8 small, triangular denticles on the outer side of the tooth.

REPRODUCTIVE SYSTEM.— (Fig. 5B) The ampulla is elongate, thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is highly convoluted and extensive. It narrows somewhat as it develops into the muscular, ejaculatory portion. The ejaculatory portion is initially narrow and gradually widens and curves over the bursa copulatrix. It then contines with another series of loops and widens into the penial bulb. The penial bulb shares a common atrium with the vagina. The distal end of the vas deferens is devoid of any penial hooks. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively thin, elongate and somewhat convoluted. It is muscular in the distal half and becomes glandular in the half closest to the genital aperture. The elongate, club-shaped receptaculum seminis joins directly to the base of the bursa. The uterine duct is short and curved and enters the female gland mass near the albumen gland.

DISCUSSION.— Bertsch (1970) described *Chromodoris baumanni* from two specimens collected from Isla San Francisco and Isla Cerralvo. Baja Californiá. México. Subsequent authors have

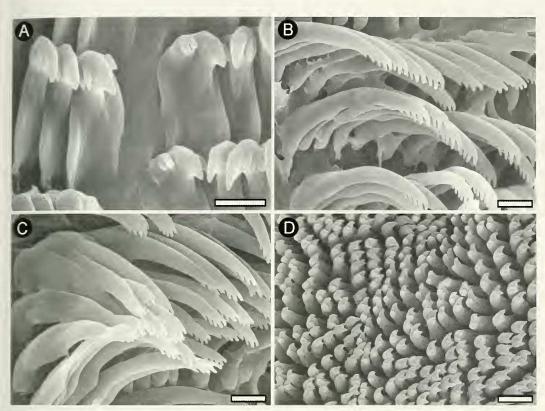


FIGURE 4. *Glossodoris baumanni* (Bertsch, 1970), scannning electron micrographs, (CASIZ 088203), Islas Secas, Gulf of Chiriquí, Panamá. A. Rachis and inner lateral teeth, scale bar = $10 \mu m$. B. Midlateral teeth from the central portion of half-row, scale bar = $10 \mu m$. C. Outer lateral teeth, scale bar = $10 \mu m$. D. Jaw rodlets, scale bar = $10 \mu m$.

identified additional material from other eastern Pacific localities from mainland México and the Galápagos Islands (Sphon and Mulliner 1972; Bertsch 1978a: Debelius 1996). More recently, Ortea et al. (1992) attributed specimens of this species from the Galápagos to Noumea haliclona (Burn, 1957). Noumea haliclona is a variably colored species that may be either pink or yellow in its body coloration and a few darker pink Its spots (Rudman 1983). rhinophores and gill are the same color as the body. This species is endemic to temperate southeastern Australia. In contrast.

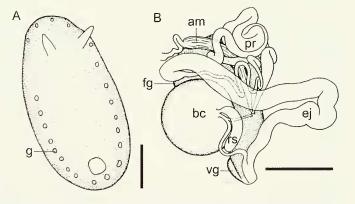


FIGURE 5. *Glossodoris baumanni* (Bertsch, 1970) A. Dorsal view of juvenile specimen showing distribution of mantle glands, g = mantle gland, scale bar = 2 mm. B. Reproductive system of mature specimen, am = ampulla; bc = bursa copulatrix; ej = ejaculatory duct; fg = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; vg = vestibular gland, scale bar = 3 mm.

Chromodoris baumanni has more numerous, smaller red pigment spots and the rhinophores and gill branches are tipped with purple pigment. Internally, *N. haliclona* has a much broader innermost lateral teeth than *C. baumanni*, with much shorter jaw rodlets. *Nounea haliclona* has a digitate vestibular gland (Rudman 1984), while that of *C. baumanni* is simple. The anatomy of specimens of *C. baumanni* examined here is entirely consistent with material described by Ortea et al. (1992) from the Galápagos Islands, with one notable exception. The reproductive system of their specimen has a small female gland mass, indicating that their specimen was not sexually mature. There is little question that the specimens that Ortea et al. (1992) attributed to *N. haliclona* are in fact *C. baumanni*.

Rudman (1984) noted that *Glossodoris* was characterized by having a convoluted mantle margin, spirally arranged gill branches on either side of the gill, a gill that vibrates rhythmically, a radular ribbon with numerous rows that is much longer than wide and an elongate, thin vaginal duct. He also suggested that species of *Chromodoris* have a straight or temporarily convoluted mantle margin, a gill without spirally arranged branches. a more squarely-shaped radular ribbon and a short muscular vagina. The only species of *Chromodoris* that is known to vibrate its gill is *C. vibrata* (Pease, 1860) (Bertsch and Johnson 1981).

Specimens of *Chromodoris bannanni* have several characteristics that are similar to species attributed to *Glossodoris*. For instance, specimens of this species have a permanently, slightly convoluted mantle margin. Also, juvenile specimens of *C. baumanni* have fewer gill branches that do not form a spiral (Fig. 1C), whereas mature specimens have well-developed spirals (Fig. 1B). Larger specimens of *C. baumanni* have been observed to have a gill plume whose branches vibrate slowly (present study), although the gill moves more slowly than in members of *Glossodoris*. The shape of the radular ribbon of *C. baumanni* is not elongate with relatively few (32–84) rows of radular teeth (Bertsch 1978a; present study), as in most species of *Chromodoris*. Rudman (1986) described several species of *Glossodoris* that had a shorter radular ribbon with fewer rows of teeth than had previously been observed. Bertsch and Gosliner (1989) also documented the presence of relatively few radular rows in *Glossodoris poliahu* Bertsch and Gosliner, 1989 and *G. tomsmithi* Bertsch and Gosliner, 1989. The vaginal duct of *C. baumanni* is thin and elongate as in species of *Glossodoris* (Rudman, 1984).

Based on the fact that most of the anatomical details of *C. banmanni* are consistent with those described for species of *Glossodoris*, this species is placed in *Glossodoris*. Detailed phylogenetic studies are needed to determine monophyletic groups within the Chromodorididae. *Hypselodoris* is the only chromodorid taxon whose monophyly has been tested with a study of its species-level phylogeny (Gosliner and Johnson 1999). The hypotheses of relationships within the Chromodorididae proposed by Rudman (1984) and Gosliner and Johnson (1999) require additional detailed study and phylogenetic analysis to further define monophyletic groups within the highly diverse chromodorid nudibranchs.

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LITERATURE CITED

- BERTSCH, H. 1970. Opisthobranchs from Isla San Francisco, Gulf of California, with the description of a new species. *Contributions in Science, Santa Barbara Museum of Natural History* 2:1–16.
- BERTSCH. H. 1977. The Chromodoridinae nudibranchs from the Pacific coast of America.— Part I. Investigative methods and supra-specific taxonomy. *The Veliger* 20(2):107–118.
- BERTSCH, H. 1978a. The Chromodoridinae nudibranchs from the Pacific coast of America.— Part II. The genus *Chromodoris*. *The Veliger* 20(4):307–327.
- BERTSCH, H. 1978b. The Chromodoridinae nudibranchs from the Pacific coast of America.— Part III. The Genera *Chromolaichma* and *Mexichromis. The Veliger* 21(1):70–86.
- BERTSCH, H. 1978c. The Chromodoridinae nudibranchs from the Pacific coast of America.— Part IV. The genus *Hypselodoris*. *The Veliger* 21(2):236–250.
- BERTSCH, H., AND T.M. GOSLINER 1989. Chromodorid nudibranchs from the Hawaiian Islands. *The Veliger* 32(3):247–265.
- BERTSCH, H., AND S. JOHNSON 1981. Hawaiian Nudibranchs: A Guide for SCUBA Divers, Snorkelers, Tidepoolers, and Aquarists. Oriental Publishing Co., Hawaii. 112 pp.
- BOUCHET, P., AND J. ORTEA. (1980) Quelques Chromodorididae bleus (Mollusca, Gastropoda, Nudibranchiata) de l'Atlantique oriental. *Annals Institute Oceanographique, Paris* 56(2):117–125.
- DEBELIUS, H. 1996. Nudibranchs and Sea Snails. Indo-Pacific Field Guide, IKAN Unterwasserarchiv. 321 pp.
- GOSLINER, TM., AND H. BERTSCH. 1988. A new species of *Mexichromis* (Nudibranchia: Chromodorididae) from the eastern Pacific. *The Veliger* 31 (1/2):127–134.
- GOSLINER, T.M., AND R.F. JOHNSON. 1999. Phylogeny of *Hypselodoris* (Nudibranchia: Chromodorididae) with a review of the monophyletic clade of Indo-Pacific species, including descriptions of twelve new species. *Zoological Journal of the Linnean Society* 125:1–114.
- ORTEA, J.A. 1988. Moluscos opistobranquios del Archipielago de Cabo Verde: Chromodorididae. *Publicações Ocasionais da Sociedade Portugesa de Malacologia* 11:1–16.
- ORTEA, J.A., J.J. BACALLADO, AND Á. VALDÉS. 1992. Resultados científicos del Proyecto Galápagos: patrimonio de la humanidad. No. 1 Chromodorididae (Mollusca: Nudibranchia). *Resultados Científicos del Proyecto Galápagos TFMC* 0-1:31–70.
- ORTEA, J.A., Á. VALDÉS, AND J.C. GARCÍA-GÓMEZ. 1996 Revisión de las especies atlánticas de la familia Chromodorididae (Mollusca: Nudibranchia) del grupo cromático azul. [Review of the Atlantic species of the family Chromodorididae (Mollusca: Nudibranchia) of the blue chromatic group.] *Avicennia* 1996(Suppl. 1):1–165.
- RUDMAN, W.B. 1983. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: Chromodoris splendida, C. aspersa and Hypselodoris placida colour groups. Zoological Journal of the Linnean Society 78:105–173
- RUDMAN, W.B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society* 81:115–273.
- RUDMAN, W.B. 1986. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: The genus *Glossodoris* Ehrenberg (= *Casella*, H. & A. Adams). *Zoological Journal of the Linnean Society* 86(2): 101–184.
- SPHON, G., AND D. MULLINER. 1972. A preliminary list of known opisthobranchs from the Galápagos Islands collected by the Ameripagos Expedition. *The Veliger* 15(2):147–152.

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